



# Phenological mismatches between above- and belowground plant responses to climate warming

Huiying Liu <sup>1,2</sup>, Hao Wang <sup>3</sup>, Nan Li <sup>1</sup>, Junjong Shao<sup>4</sup>, Xuhui Zhou <sup>1,5</sup> ✉, Kees Jan van Groenigen <sup>6</sup> and Madhav P. Thakur <sup>7</sup>

**Climate warming is changing the aboveground phenology of plants around the world. However, the effects of warming on the belowground phenology of plants remain relatively under-investigated, even though roots play a vital role in carbon cycling. Here we synthesize 88 published studies to show a phenological mismatch between above- and belowground plant responses to climate warming. For herbaceous plants, warming advanced both the start and end of aboveground growing season, resulting in an unchanged growing season length. In contrast, belowground phenophases (the start, end and length of the growing season) of herbaceous plants remained unchanged. For woody plants, climate warming did not affect any aboveground phenophases but extended their belowground growing season. Mismatches between above- and belowground phenology will strongly influence biomass allocation in plants, implying that terrestrial carbon cycling models based exclusively on aboveground responses are inaccurate. The work highlights an urgent need for future research of under-represented belowground phenological changes.**

The timing of life-history events of organisms (that is, phenology) is crucial for their fitness and survival<sup>1,2</sup>. There is an increasing consensus that anthropogenic climate change has shifted the phenology of many organisms, which may adversely affect ecosystem functioning and stability<sup>3,4</sup>. Our current understanding of plant phenological shifts to climate warming relies heavily on research centred on the aboveground part of plants<sup>5,6</sup>. Accordingly, terrestrial biosphere models (for example, CLM 4.0, BIOME-BGC and Sheffield-DGVM) use aboveground plant phenology as a surrogate of whole-plant phenology<sup>7,8</sup>. However, belowground plant biomass also plays a key role in numerous ecosystem processes. For instance, root growth can account for up to 67% of net primary productivity (NPP) in terrestrial ecosystems<sup>9</sup>. Roots also control evapotranspiration rates and water transport within soils<sup>10</sup>, and play a key role in determining soil structure<sup>11,12</sup>.

Different phenological responses to climate change have been well reported across trophic levels<sup>13,14</sup>, but phenological mismatches can also occur within a single organism. So far, how belowground plant phenology responds to climate warming and whether those responses match shifts in aboveground plant phenology remain understudied<sup>15,16</sup>. Based on functional equilibrium theory, which indicates plastic changes in above- and belowground growth in response to environmental variation<sup>17</sup>, similar shifts in above- and belowground plant phenology under global warming can be expected due to their physiological coupling. However, recent experimental evidence suggests that their responses might differ<sup>16,18</sup>. The underlying reasons for such a mismatch are unknown but may be related to competition for limited resources between various life forms of plants, and how climate warming alters those resources<sup>19</sup>.

For instance, woody plants generally face stronger aboveground competition for light availability, whereas herbaceous plants face stronger belowground competition for soil nutrients<sup>20</sup>. Given our limited understanding of belowground phenological responses to warming, model predictions of ecosystem processes (for example, soil carbon dynamics) to climate change that rely exclusively on aboveground phenology could be inaccurate.

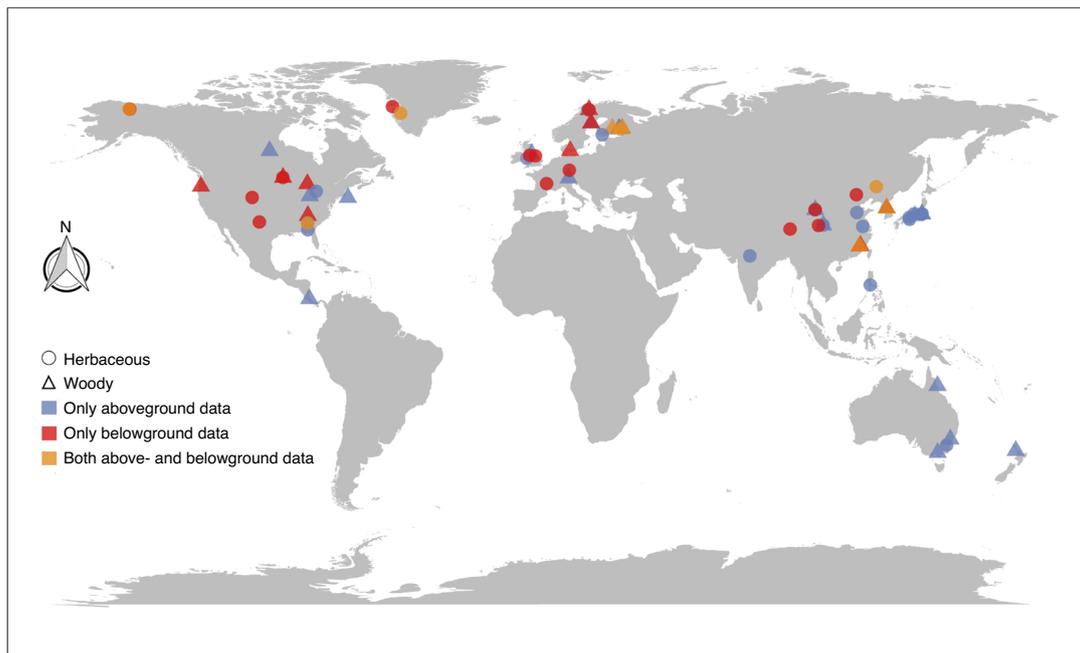
Here, we aim to determine how climate warming alters above- and belowground plant phenology, and whether these responses are synchronized. We also investigate mechanisms underlying the match (or mismatch) in responses between above- and belowground plant phenology. Towards this end, we performed a global meta-analysis of 88 independent studies from 19 countries including 281 and 106 observations for above- and belowground phenology, respectively, to find general patterns of phenological responses of herbaceous and woody plants to experimental warming (Fig. 1). Our results provide compelling evidence for mismatches between above- and belowground plant phenology, and identify differences in phenological responses between herbaceous and woody plants to climate warming.

## Warming effects on above- and belowground phenology

Averaged across our dataset, climate warming shifted both the start and end of the aboveground growing season towards spring, without significantly changing the growing season length. In contrast, belowground phenophases including the start, end and length of the growing season did not change significantly with warming (Fig. 2a,d,g).

The above- and belowground responses differed between plant growth forms and biomes. For herbaceous plants (43 species),

<sup>1</sup>Tiantong National Station for Forest Ecosystem Research, Center for Global Change and Ecological Forecasting, The Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China. <sup>2</sup>Institute of Eco-Chongming (IEC), Shanghai, China. <sup>3</sup>State Key Laboratory of Grassland and Agro-ecosystems, Institute of Innovation Ecology, Lanzhou University, Lanzhou, China. <sup>4</sup>College of Forestry and Biotechnology, Zhejiang A&F University, Hangzhou, China. <sup>5</sup>Center for Ecological Research, Key Laboratory of Sustainable Forest Ecosystem Management-Ministry of Education, School of Forestry, Northeast Forestry University, Harbin, China. <sup>6</sup>Department of Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK. <sup>7</sup>Terrestrial Ecology Group, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland. ✉e-mail: [xzhou@nefu.edu.cn](mailto:xzhou@nefu.edu.cn)



**Fig. 1 | Global distribution of warming experiments included in this meta-analysis.** Circles and triangles indicate experiments on herbaceous and woody plants, respectively. Blue, red and orange colours indicate, respectively, sites contributing aboveground data, belowground data and both above- and belowground data to the dataset.

climate warming significantly advanced the start and end of the aboveground growing season by 1.31 days per °C (95% CI  $-1.80$  to  $-0.82$  days per °C) and 1.80 days per °C (95% CI  $-2.60$  to  $-1.02$  days per °C) (Fig. 2b,e and Supplementary Table 1), respectively, resulting in an unchanged length of growing season (Fig. 2h). In contrast, warming did not affect the start, end or length of the belowground growing season (Fig. 2b,e,h, all  $P > 0.05$ ). When herbaceous plants were separated into grasses and forbs, both groups showed similar phenological responses to warming (Supplementary Fig. 1).

For woody plants (38 species), climate warming did not significantly affect the start, end or length of the aboveground growing season (Fig. 2c,f,i). However, warming significantly advanced the start of the belowground growing season by 1.28 days per °C (95% CI  $-2.20$  to  $-0.36$  days per °C) but did not affect the end of growing season, thereby extending the growing season length by 2.25 days per °C (95% CI 0.84 to 3.66 days per °C) (Supplementary Table 1). When woody plants were further divided into trees and shrubs, the responses of these two groups were consistent with the overall response, with stronger responses of below- than aboveground phenophases (Supplementary Fig. 1). Deciduous woody plants showed delayed start and shortened length of the aboveground growing season compared with evergreen woody plants, which showed no significant response to warming (Supplementary Fig. 1).

Grasslands and farmlands, both of which are dominated by herbaceous plants, responded similarly to climate warming, with aboveground phenophases responding more strongly to warming than belowground ones. Forests and shrublands (dominated by trees and shrubs) showed more sensitive responses to climate warming for below- than aboveground phenophases (Supplementary Fig. 1). These patterns remained when the analysis was restricted to studies that monitored above- and belowground phenology simultaneously (Supplementary Fig. 2). In addition, the simultaneous monitoring data reveal that existing differences in the end of above- and belowground growing season may become even more pronounced, whereas those in the start of above- and belowground growing season remain similar (Supplementary Fig. 3).

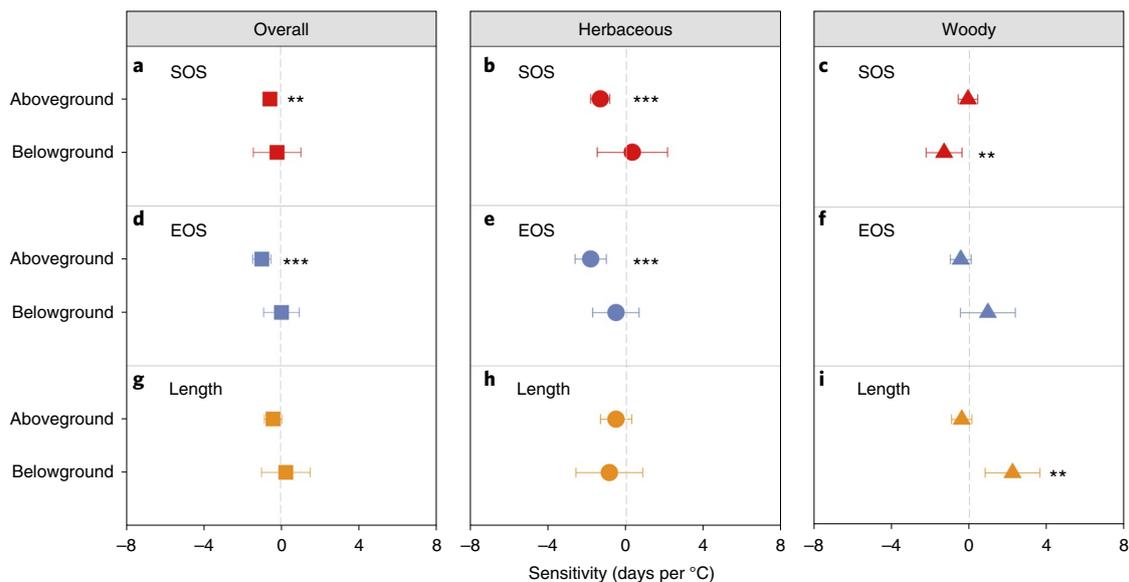
### Environmental and ecological drivers

For herbaceous plants, the advancement of the start of the aboveground growing season per degree of warming became less pronounced with increasing leaf nitrogen content and with warming magnitude (Fig. 3a–c). The effect of warming on the end of the aboveground growing season was strongly affected by warming magnitude and by warming-induced changes to the start of the growing season (Fig. 3e). Warming-induced advancements of the end of the aboveground growing season became smaller with increasing warming magnitude, and advancements in the start were related to an earlier end of the aboveground growing season (Fig. 3f,g). Although a random forest analysis identified wetness index as the most important predictor for the start of the belowground growing season (Fig. 3d), meta-regression analysis did not detect any significant relationships. The response of the end of the belowground growing season to warming was most strongly affected by warming-induced changes in the start of the belowground growing season and by plant height (Fig. 3h,i). Warming-induced delays in the end of the growing season became smaller with increasing plant height and turned into advancements for tall plants (Fig. 3j).

For woody plants, the start and end of the aboveground growing season both advanced with the extension of experimental duration (Fig. 4a,f), with greater phenological advancements (more negative sensitivity values) for longer experiments (Fig. 4b,g). The temperature sensitivity of the end of the aboveground growing season positively correlated with that of the start of the growing season (Fig. 4h). The start of the belowground growing season was affected by climatic factors (Fig. 4c), with larger advancements for warmer and wetter climates (Fig. 4d,e). However, the delay in the end of the belowground growing season was mostly affected by NPP (Fig. 4i). More specifically, the end of the belowground growing season tended to be delayed by warming when NPP was small but to be advanced when NPP was large (Fig. 4j).

### Discussion

Understanding warming-induced phenological shifts in organisms is key to advancing climate change biology. Several recent studies



**Fig. 2 | Temperature sensitivity of above- and belowground phenophases to experimental warming.** **a–i**, Temperature sensitivity of start of growing season (SOS; **a–c**), end of growing season (EOS; **d–f**) and length of growing season (**g–i**) for all plants (aboveground,  $n = 281$ ; belowground,  $n = 106$ ; **a,d,g**), herbaceous plants (aboveground,  $n = 120$ ; belowground,  $n = 69$ ; **b,e,h**) and woody plants (aboveground,  $n = 161$ ; belowground,  $n = 37$ ; **c,f,i**) with 95% CI (error bars) and effect size of zero (vertical dashed line). Treatment effects considered significant if the 95% CI of the effect size does not overlap with zero. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

have pointed out that shifts in plant phenology under climate change can alter ecosystem functions<sup>4,21–23</sup>. Our global synthesis provides two main novel findings to improve our understanding of plant phenology in a changing world. First, we demonstrate that, even within the same life forms of plants, warming can cause mismatches between above- and belowground plant phenology. Second, the effect of warming on belowground phenology differs between two major life forms of plants. That is, the belowground phenology of herbaceous plants was less sensitive to warming than that of woody plants. Such mismatches can have far-reaching consequences for ecosystem stability and functioning, such as terrestrial carbon balance and mass and energy flow between above- and belowground compartments<sup>22</sup>.

For herbaceous plants, aboveground phenophases were more sensitive to climate warming than belowground ones. The advanced start of aboveground growing seasons in herbaceous plants confirms findings of previous studies, and can be explained by warming-induced advancing of the accumulated temperature requirements in plants<sup>6,24</sup>. The earlier start of the growing season also resulted in an earlier end of the growing season, potentially because of the limited leaf longevity and programmed cell death in plants<sup>25,26</sup>. Our finding that changes in aboveground phenophases slowed down with warming magnitude may be related to unfulfilled chilling requirements or photoperiod limitations under warmer climates<sup>27,28</sup>.

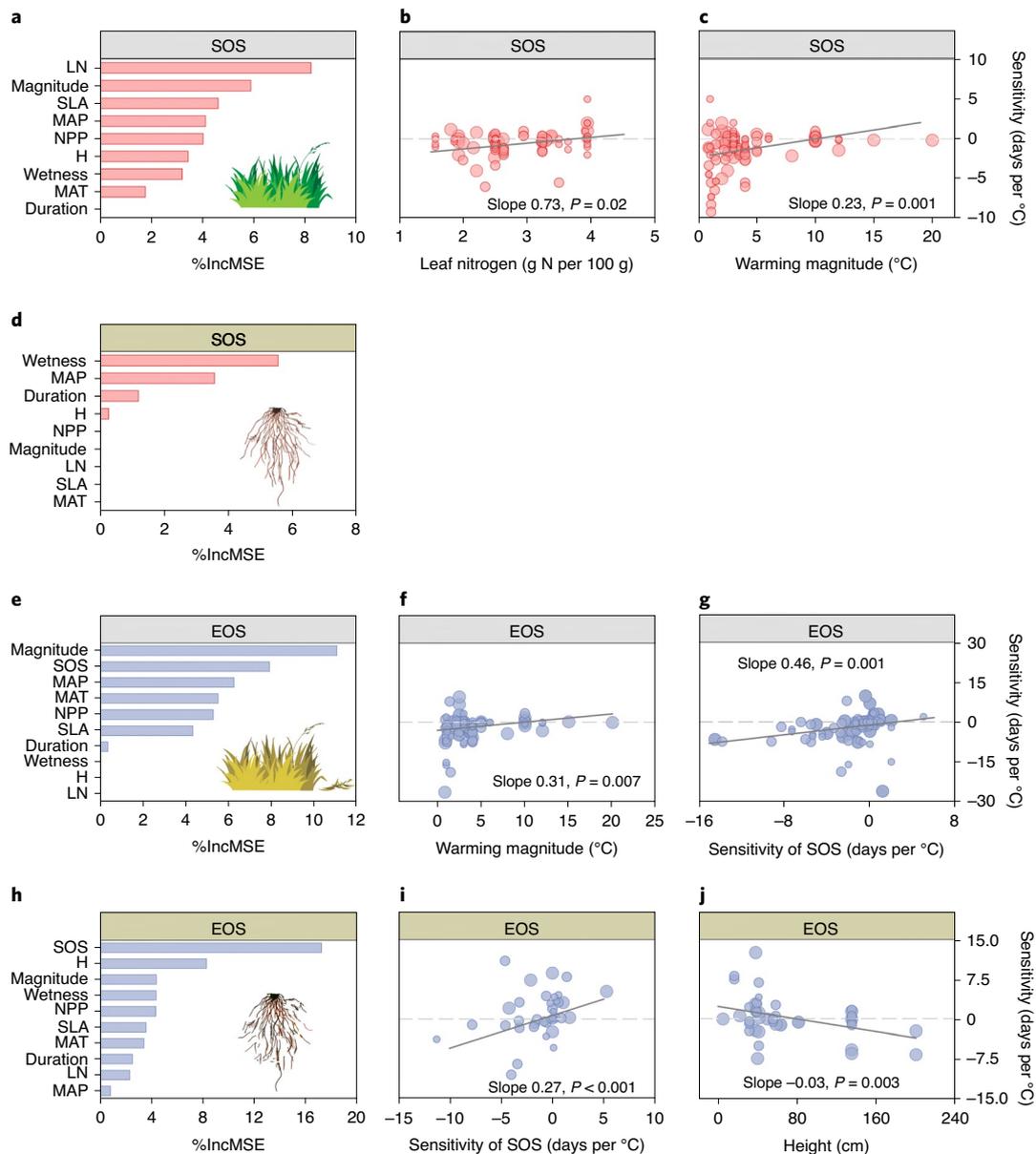
In contrast to proposals that physiology links above- and belowground phenology<sup>17</sup>, the earlier start of the aboveground growing season did not translate into an earlier start of the belowground growing season. This may be attributed to the fact that the start of the above- and belowground growing season is driven by various types of endogenous and exogenous cues<sup>15</sup>. The start of the aboveground growing season can primarily be affected by air temperature<sup>29</sup>, whereas the start of the belowground growing season may be controlled by more complex factors, such as stored carbohydrates and plant growth regulators (for example, auxins and cytokinins)<sup>15,30</sup>. Furthermore, a lack of soil moisture may inhibit belowground responses to warming because herbaceous plants

often grow in relatively arid areas<sup>31</sup>. Finally, thermal insulation by soil may also contribute to a weaker response of belowground phenophases in herbaceous plants<sup>15,22</sup>. This hypothesis deserves further examination in future experimental studies of plant phenology.

The early termination of aboveground growing seasons and the unaltered end of belowground growing seasons in herbaceous plants may also reflect different strategies to cope with warming effects. For instance, when warming advances the start of the growing season, a plant's demand for nutrients and water will increase earlier in the year<sup>32</sup>. As a result, soil nutrient pools may become depleted by the end of the growing season in nutrient-limited ecosystems. In such cases, aboveground plant production slows down, or senescence starts earlier<sup>33</sup>. By contrast, warming may not slow down belowground biomass production or advance the end of the belowground growing season, because plants tend to allocate more photosynthetic products belowground to acquire limiting resources during the growing season<sup>34</sup>.

Our finding that warming did not affect the length of the aboveground growing season for herbaceous plants is in contrast with previous studies<sup>35,36</sup>. This apparent inconsistency probably reflects a difference in methodological approach. Phenophases such as leaf-out and leaf senescence are generally determined by satellite-derived normalized difference vegetation index data or field monitoring<sup>6,37</sup>, while our study used seasonal biomass dynamics to determine phenophases for improving the comparison between the above- and belowground plant phenology. Phenological indicators observed by different methods could be differentially affected by environmental conditions<sup>38</sup>, which may have contributed to this contrasting result. For instance, plants can leaf out around 0 °C, but they can only accumulate biomass rapidly when air temperature is higher than 5 °C (ref. <sup>38</sup>).

For woody plants, belowground phenophases were more sensitive to climate warming than aboveground ones. Compared with herbaceous plants, woody plants have deeper root distributions and higher water use efficiency<sup>39,40</sup>, which could make woody plants benefit more when warming-induced water stress occurs. The prolonged belowground growing season and the unchanged

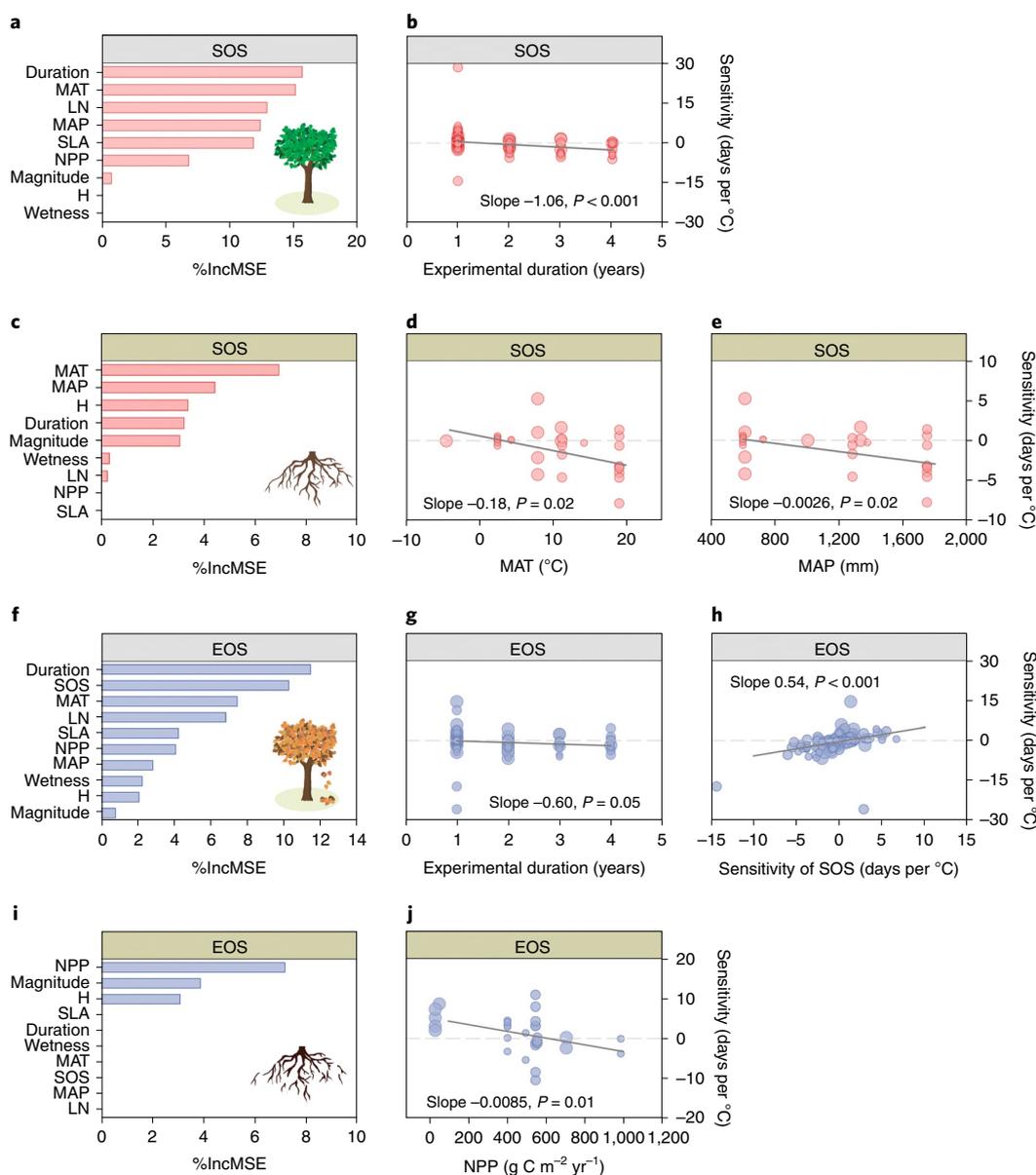


**Fig. 3 | Key predictors explaining temperature sensitivity of phenophases for herbaceous plants. a–c,** Start of aboveground growing season. **d,** Start of belowground growing season. **e–g,** End of aboveground growing season. **h–j,** End of belowground growing season. The importance of predictors was determined by using the %IncMSE derived from random forest; negative values of the relative importance, which indicate lack of importance, are not shown. Negative temperature sensitivity values indicate advancements of phenological stages, whereas positive values indicate delays. The size of the circles is proportional to the weights of the observation. MAP, mean annual precipitation; MAT, mean annual temperature; Wetness, wetness index; Magnitude, warming magnitude; Duration, experimental duration; H, plant height; SLA, specific leaf area; LN, leaf nitrogen; SOS, start of growing season; EOS, end of growing season.

aboveground growing season of woody plants indicated that plants allocated more resources to belowground than aboveground organs under warming, possibly reflecting the increased need for nutrients and water to sustain increased NPP with warming<sup>34</sup>. The warming-induced advancements of the start and end of growing season became stronger over time, consistent with flowering phenology observed in tundra regions under warming<sup>41</sup>. We present two possible explanations for this finding. First, woody plants may accumulate a nutrient reservoir over time, including non-structural carbohydrates, which may promote a more positive response of plant phenology to warming through nutrient and carbohydrate supply<sup>42</sup>. Second, consistent with the ‘transient maxima hypothesis’<sup>43</sup>, which proposes a short-term elevated response under

non-equilibrium conditions when resource availability varies, an enhanced phenological response within a relatively short term in our study is logical. Long-term studies are still needed to confirm whether this pattern of advanced start and end of the growing season holds over time.

Interestingly, we found that warming delayed the end of the belowground growing season of both woody and herbaceous plants when NPP or plant height was low, but advanced the end of the growing season when NPP or plant height was high (Figs. 3j and 4j). These results may reflect the role of plant competition for limited resources in mediating warming effects on the belowground phenophases. At low NPP values, low intensity of competition and warming-induced increases in nutrient availability may allow plants



**Fig. 4 | Key predictors explaining temperature sensitivity of phenophases for woody plants. a, b**, Start of aboveground growing season. **c–e**, Start of belowground growing season. **f–h**, End of aboveground growing season. **i, j**, End of belowground growing season. Importance values determined by using %IncMSE derived from random forest analysis.

to absorb more nutrients to resist frost damage<sup>44</sup>, thereby postponing the end of the growing season<sup>45</sup>. However, increases in belowground NPP under climate warming may aggravate competition intensity when NPP or plant height is already high, causing plants to die earlier<sup>46,47</sup>. Resource-driven shifts in above- and belowground plant phenology with climate warming merit further exploration in climate change studies.

Understanding the links between above- and belowground phenology is crucial for predicting whole ecosystem responses in a warming world. Our meta-analysis provides compelling evidence of mismatches between above- and belowground plant phenology<sup>5,16</sup> and identifies the magnitude of those differences between herbaceous and woody plants. More importantly, our results suggest that aboveground plant phenology is a poor proxy for belowground plant phenology. Nonetheless, most contemporary Earth system models still assume a fixed leaf-to-root allocation to simulate

carbon, water and energy fluxes<sup>7,8</sup>, which implies synchrony between above- and belowground plant phenology. Thus, our results call for the explicit incorporation of belowground plant phenology into next-generation Earth system models, as it may respond differently to aboveground plant phenology. Predictions of carbon dynamics in terrestrial ecosystems in response to anthropogenic climate change may also be improved by accounting for differences between woody and non-woody plants. Although we have evaluated the mismatch between above- and belowground plant phenology at the global scale, we could still only examine a handful of species that are distributed in 19 countries. Plant phenology data from regions such as Africa and South America are still unavailable. Thus, a dearth of studies on above- and belowground plant phenology still constrains our ability to generate global prediction of terrestrial plant phenology in response to climate warming. Nevertheless, our results encourage future studies to examine both the causes and

consequences of phenological mismatches in above- and below-ground plant phenology in response to climate warming.

### Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-021-01244-x>.

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## Methods

We used meta-analysis to assess the effects of experimental warming on above- and belowground plant phenology. We searched for journal articles using the ISI Web of Science with the following key word combinations: (warming OR temperature OR climate change) AND (root production OR root mortality OR root turnover OR standing biomass OR root longevity OR standing crop OR root length OR lifespan OR root phenology) AND (shoot length OR net primary productivity OR biomass OR growth OR shoot elongation) from 1980 to 2020. Papers had to meet the following criteria to be included in our dataset: (i) warming experiments were conducted in terrestrial ecosystems; (ii) initial environmental, soil, and plant conditions, including climate, soil type and species composition in control plots were the same as those in warming plots; (iii) at least two temperature regimes were compared. We acquired data regarding plant growth dynamics directly from text or tables in original papers or extracted data indirectly from figures by using GetData software (version 2.22). In total, our dataset included 359 observations from 88 studies. Among these observations, there were 281 aboveground phenological observations and 106 belowground phenological observations (Fig. 1 and Supplementary Fig. 4). To ensure that our search captured all relevant studies, we repeated our literature search using Google Scholar and ordered the studies by relevance; all studies in the top 200 found by Google Scholar that met our criteria were already included in our dataset.

Ancillary site information including latitude, longitude, annual mean air temperature and mean annual precipitation were also compiled. Annual mean air temperature and annual precipitation were taken directly from the original study, or from papers cited in that study. If these data were not presented, we extracted them from the WorldClim database ([www.worldclim.com](http://www.worldclim.com))<sup>48</sup>.

**Phenological parameter extraction.** Similar to previous studies<sup>49,50</sup>, the start and end of the aboveground growing season were defined as the Julian days at which 10% and 90% of annual growth in aboveground dry matter, plant height or stem diameter were accumulated, while those of the belowground growing season were defined as the Julian days when 10% and 90% of annual peak growth in root dry matter or root length were accumulated (Supplementary Fig. 5). For our dataset, 79% of the aboveground phenological parameters of herbaceous plants were extracted from aboveground biomass dynamics, and 76% of the aboveground phenological parameters of woody plants were extracted from plant height dynamics or shoot length dynamics. Most of the belowground phenological parameters were extracted from studies using nondestructive minirhizotron methods; only one study used rhizotrons, while one study used the root collar diameter method to monitor root growth dynamics. The sampling frequency was at least four times per growing season for aboveground biomass and once around every 2–4 weeks for root growth dynamics. Here, we used the production between the first and last sampling time within a year as the annual production. Before extracting the phenological parameters, we standardized production at the sampling dates by subtracting the production at the first sampling date to remove the effects of pre-year production.

**Statistical analysis.** To account for the differences in warming magnitude between studies, we used temperature sensitivity (that is, days per °C)<sup>19,29</sup> to assess warming effects on plant phenology:

$$\text{Temperature sensitivity} = (X_w - X_c)/\Delta T, \quad (1)$$

where  $X_w$  and  $X_c$  are mean values of plant phenological parameters (that is, start, end and length of the growing season) in warming and control plots, respectively, and  $\Delta T$  is the temperature difference between warming and control plots.

We weighted studies by the number of replicates<sup>51</sup>:

$$W_r = (N_c \times N_w)/(N_c + N_w) \quad (2)$$

where  $W_r$  is the weight assigned to each observation, and  $N_c$  and  $N_w$  are the number of replicates for ambient and elevated temperature treatments, respectively.

We used the 'rma.mv' function in the 'metafor' package (version 3.0-2) in R software to calculate weighted effect sizes and their 95% confidence intervals<sup>52</sup>. The meta-analysis model included the variable 'publication' as a random factor, as some studies resulted in more than one effect size. Warming effects on plant phenological parameters were considered to be statistically significant when the 95% confidence intervals of effect sizes did not overlap with 0.

We included mean annual temperature (MAT), mean annual precipitation (MAP), wetness index, warming magnitude, experimental duration, NPP, specific leaf area, plant height and leaf nitrogen ([www.try-db.org](http://www.try-db.org))<sup>53</sup> to predict the start of growing season for both above- and belowground plant responses (Supplementary Table 2). Wetness index was calculated as<sup>54</sup>

$$\text{Wetness index} = \frac{\text{MAP}}{\text{MAT} + 10} \quad (3)$$

As the start of growing season could affect the end of growing season, we also added the start of growing season as a predictor of the end of growing season.

Random forest ('randomForest' (version 4.6-14) package in R software<sup>55</sup>) was used to rank the predictors in order of importance following the method from refs. <sup>56,57</sup>. The ranking method is based on mean decrease in mean square error (%IncMSE). The higher the value, the more important the predictors in affecting the sensitivity of the plant phenophases. Negative %IncMSE values indicate that the model predictions are better without including the specific predictor, thus the predictor is less important<sup>56</sup>. After ranking the relative importance, we used a between-group Q statistical test to compare the relationships between the temperature sensitivity of phenological events and different predictors. When we analysed the relationships of the temperature sensitivity of phenological parameters with MAT, MAP and NPP, only the data from field experiments were included, even though field and laboratory studies did not yield different results for most phenological parameters (Supplementary Fig. 6). Egger's regression and fail-safe analysis were used to test the publication bias (Supplementary Table 3). All the statistical analyses were conducted in R 4.1.1. The global map was produced using the R package 'ggplot2'<sup>58</sup>.

## Data availability

The data used in the current study are available in the Figshare repository: <https://figshare.com/s/1f086364114021cd80d9><sup>59</sup>.

## Code availability

The data analysis was carried out in R 3.6.1. The complete codes used to generate the results reported in this study are available in the Figshare repository: <https://figshare.com/s/1f086364114021cd80d9><sup>59</sup>.

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## Author contributions

H.L. and H.W. developed the idea, analysed the data and wrote the manuscript with substantial input from M.P.T. and X.Z. All authors contributed to the writing of the paper.

## Competing interests

The authors declare no competing interests.

## Additional information

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**Correspondence and requests for materials** should be addressed to Xuhui Zhou.

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